

# Aspects of Reproduction in Some Enoploteuthid Squids from Hawaiian Waters<sup>1</sup>

by

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*Abstract.* This study investigates aspects of reproduction of three enoploteuthid squid species, *Pterygioteuthis microlampas* Berry, *Pyroteuthis addolux* Young, and *Abraliopsis* sp., captured in Hawaiian waters during a 17-month, midwater-trawl sampling program. *Pterygioteuthis microlampas* differed from the other species in having smaller ova and higher relative fecundity. Juveniles of *P. microlampas* were most often caught in spring months, indicating a seasonal spawning tendency in this species. Seasonality of spawning in one or more species also was indicated by fall and winter peaks in enoploteuthid larval abundance. Although the majority of females in the larger size classes had mated prior to capture, only a minority of ova in any specimen were mature and the ratios of female gonad dry weight to total body dry weight were generally low, suggesting that full reproductive maturity was not observed in these specimens. In light of these results, net avoidance is considered, as is the possibility that partially spent females were captured. Also raised is the question of whether these species are able to spawn in more than one spawning season.

## INTRODUCTION

APPROXIMATELY 50 species of pelagic squid are known to occur in Hawaiian waters (YOUNG, 1978). Most of these are small in size and low in abundance. Those most commonly captured in mesopelagic trawl samples are of the family Enoploteuthidae. Previous studies of enoploteuthid species in Hawaii have primarily involved their systematics (BERRY, 1914), vertical distribution (YOUNG *et al.*, 1980; YOUNG, 1978; ROPER & YOUNG, 1975), photobiology (YOUNG *et al.*, 1980; YOUNG, 1972, 1973), and occurrence in the diet of larger carnivores (KING & IKEHARA, 1956; CLARKE, 1971). A few papers have treated aspects of reproduction of enoploteuthids occurring in temperate waters (*e.g.*, SASAKI, 1914; OKUTANI & MCGOWAN, 1969; PEARCY, 1965). However, the life histories and reproductive biology of the Enoploteuthidae remain largely unstudied.

The following study was undertaken to investigate fecundity, size at maturity, larval abundance, seasonality, and other aspects of reproduction of the three most commonly sampled enoploteuthid squid species in Hawaiian waters. Many of the results must be considered prelimi-

nary due to the sampling difficulties inherent in studies of this kind. Nevertheless, this study contributes original data that provide new insights into the life histories of these little-known squid species.

## MATERIALS AND METHODS

This study is based primarily on specimens collected at approximately monthly intervals 20 km west of Oahu, Hawaii, between August, 1977, and October, 1978. Juvenile and adult enoploteuthids were collected in nighttime oblique samples with a 3-m Isaccs-Kidd midwater trawl (IKMT) and a 1.25-m diameter bongo net (BB). Larvae ( $\leq 5$  mm dorsal mantle length) were taken primarily in standard bongo nets (SB) of 70-cm diameter. Each net was equipped with a flow meter and a time-depth recorder. The IKMT had a mouth area of 7.7 m<sup>2</sup> and a mesh of about 6 mm, except for a 1-m cod end of 333  $\mu$ m. The IKMT was towed at 2 m/s and was retrieved at 40–50 m/min. The average maximum depth reached was 325 m ( $\pm 30$  m), and the average volume filtered per tow was  $101 \times 10^3$  m<sup>3</sup>. The BB mesh was 2.5 mm. It was towed at about 1.75 m/s and retrieved at 40–50 m/min. The average maximum depth was 304 m ( $\pm 6$  m), and average volume filtered per net was 9434 m<sup>3</sup>. The standard bongo was towed at 1 m/s and retrieved at a

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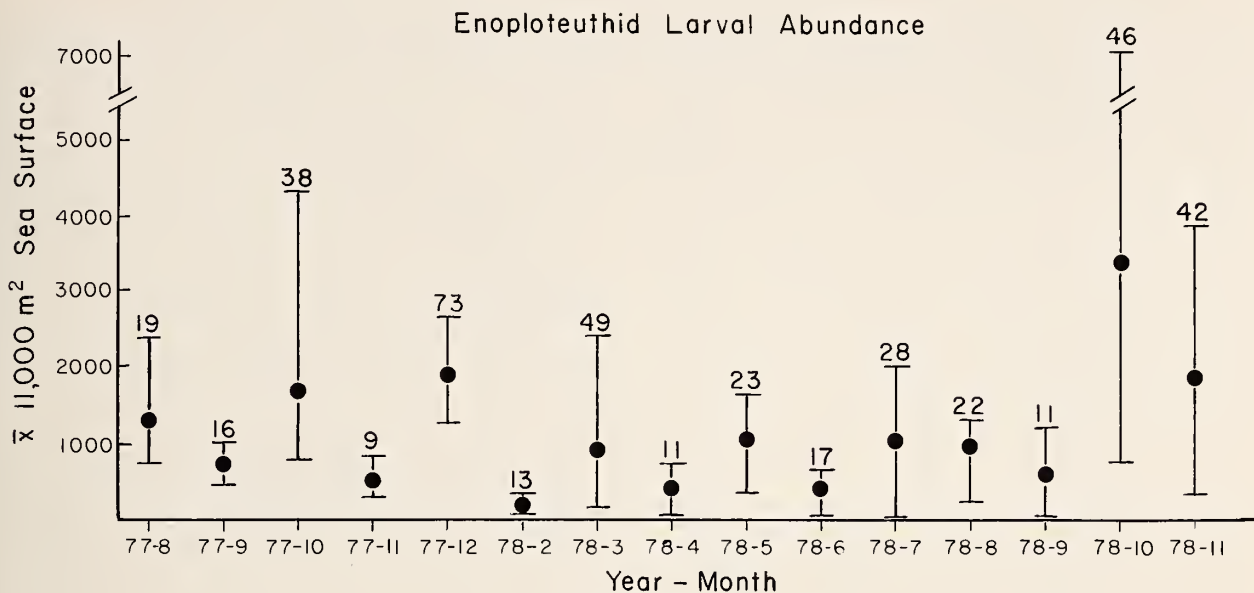


Figure 1

Monthly abundance estimates of enoploteuthid squid larvae ( $\bar{x}/1000 \text{ m}^2$  of sea surface area) as determined by nighttime standard bongo tows. Mean values and ranges are indicated;  $n$  = number of larvae ( $\leq 5 \text{ mm DML}$ ) captured.

rate of 60 m/min. The average maximum depth attained was 224 m ( $\pm 33 \text{ m}$ ) and average volume filtered was 790  $\text{m}^3$  per net. For each tow, it was assumed that the entire sampled population occurred above the maximum depth attained by these nets. This assumption is supported by the vertical distribution study of YOUNG (1978). For each month, except January, 1978, when no samples were collected, 3-4 replicate IKMT tows, 2-4 standard bongo tows, and 2 large bongo tows were taken.

All samples were preserved in 10% formalin. Squid larvae from standard bongo tows were identified to family. For each SB tow, the number of enoploteuthid squid larvae per 1000  $\text{m}^2$  of sea surface area was estimated (after MAYNARD *et al.*, 1975) by multiplying the number of larvae captured by 1000  $\times$  (maximum net depth/volume filtered).

Adult and juvenile enoploteuthids from BB and IKMT tows were identified to species, sexed, and dorsal mantle length (DML) measured. Specimens from IKMT catches were pooled by quarter to consider seasonal trends in size composition. K-S tests (SIEGEL, 1956) were used to estimate the significance of differences observed in the size frequency curves of *Pterygioteuthis microlampas* Berry, 1913, sampled in four seasons.

Ovaries were examined and extracted from adult and juvenile ( $\geq 9 \text{ mm DML}$ ) specimens of *Pterygioteuthis microlampas*, *Pyroteuthis addolux* Young, 1972, and *Abraliopsis* sp. B (nomenclatural usage follows YOUNG, 1978). Gonad dry weight/total body dry weight ratios (G/S) were determined for all dissected specimens after drying for 24 h at 60°C.

Fecundity estimates were made for 10 or more of the largest specimens of each of the three species on the assumption that the larger specimens would contain the greatest numbers of mature ova. Individual fecundity was determined by direct count of all yolked oocytes. Oocytes were considered to be yolked if their nuclei were not discernible at 10 $\times$  magnification. Relative fecundity, expressed as ova/g total dry weight, was used for interspecific comparisons. Mann-Whitney tests (ZAR, 1974) were used to estimate the significance of differences in relative fecundity.

Ova size-distribution frequencies were determined by manual dissection of the ovaries and examination of samples with a microscope. Several methods were used to sample the ovary in an effort to develop a reliable and accurate technique. In a total of nine specimens representing all three species, sections were examined from the most posterior and anterior ends of the ovary, and from the midsection. For most other specimens, only the posterior terminus of the ovary was examined. The entire ovary was examined in one specimen each of *Abraliopsis* sp. B and *Pterygioteuthis microlampas*. In three *Pyroteuthis addolux*, the entire ovary was gently teased apart and mixed, and several samples were examined.

## RESULTS

The most commonly collected squid in 57 IKMT and 28 BB tows were the enoploteuthid species *Pterygioteuthis microlampas*, *Pyroteuthis addolux*, and *Abraliopsis* sp. B. One hundred and sixteen adult and juvenile ( $\geq 9 \text{ mm}$

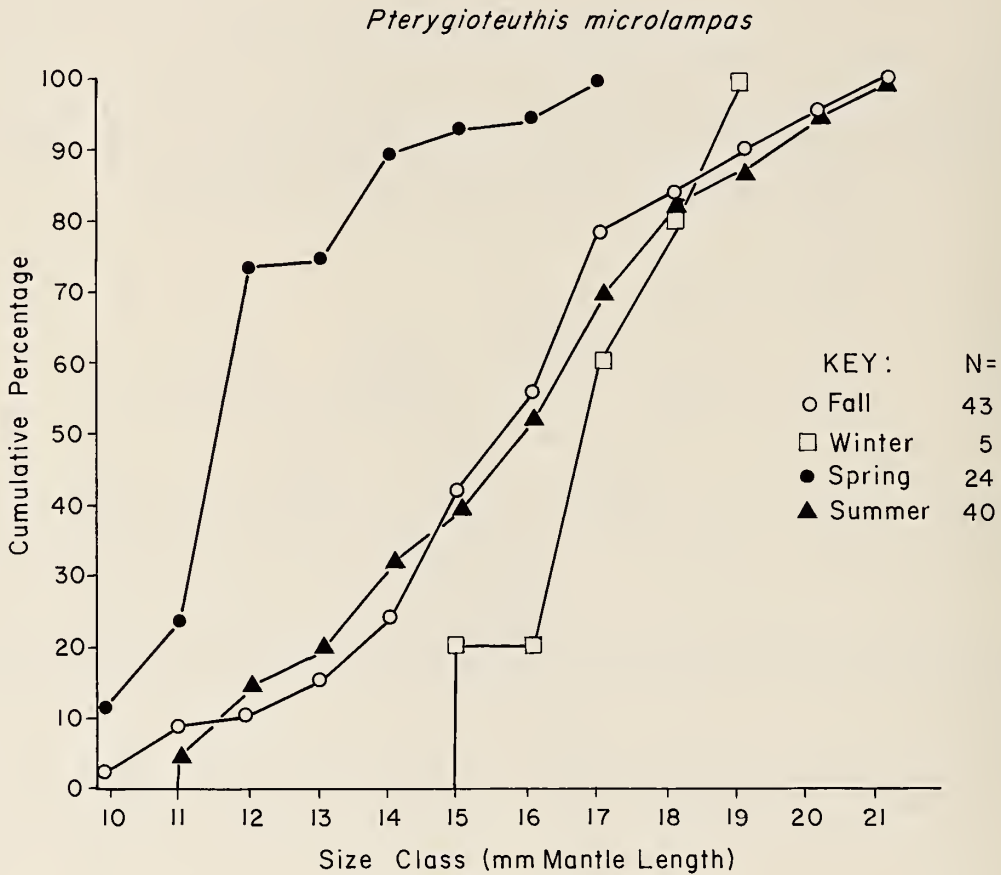


Figure 2

Cumulative size class percentages of *Pterygioteuthis microlampas* sampled by IKMT in four seasons. The spring size-class distribution differs significantly from each of the others ( $P < .01$ , K-S test);  $n$  = number of specimens captured.

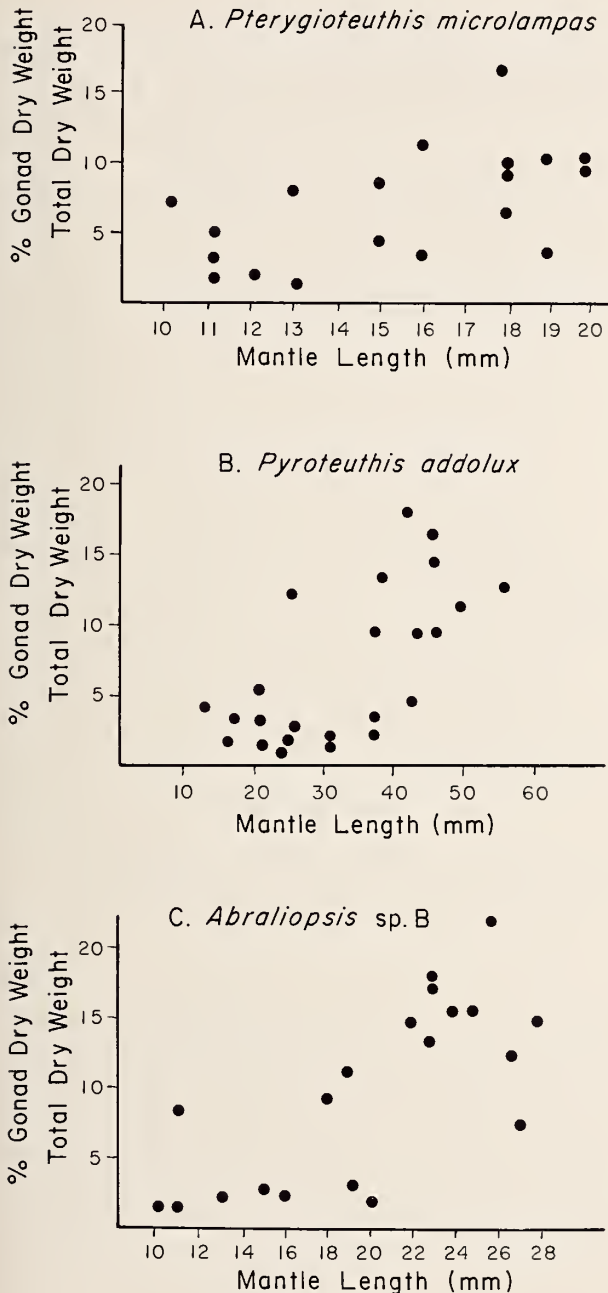
DML) *P. microlampas*, 88 *P. addolux*, 51 *Abraliopsis* sp. B, 48 *Pterygioteuthis giardi* Fischer, 1895, 26 *Abraliopsis* sp. A (after YOUNG, 1978), and 13 *Abralia trigonura* Berry, 1913, were collected.

Enoploteuthid larvae were present all year (Figure 1). The greatest abundances of larvae occurred during the months of October and December, 1977, and October and November, 1978, indicating the possibility of a seasonal spawning trend in one or more species. The large ranges observed in larval abundance estimates by the individual tows are probably due to the low average number of larvae captured per tow, but may also indicate patchiness of distribution.

The data for *Pterygioteuthis microlampas* (Figure 2) indicate that 90% were  $\leq 14$  mm in spring, that all sizes were more nearly equally represented in summer and fall, and that only animals  $\geq 15$  mm were found in winter. The size-frequency curve for spring differed significantly ( $P < .01$ , K-S test) from that of each of the other seasons,

but no significant differences ( $P > .05$ ) were found among the other seasonal pairs. The absence of a significant difference between winter and spring or fall may have been the result of the smaller number ( $n = 5$ ) of specimens collected in winter. *Pyroteuthis addolux* and *Abraliopsis* sp. B showed no coherent seasonal changes in size distribution.

The ratios of female gonad dry weight to total dry weight (G/S) were plotted against mantle length for the three species to estimate length at onset of reproductive maturity (Figures 3a, b, c). Increasing G/S ratios were not strictly correlated with increasing mantle length in any species, indicating that the onset of sexual maturity is not strictly size dependent, or that partially spent or spawning females may have been captured. The maximum G/S ratios for each species were found, not in the largest specimens, but in an 18-mm (DML) *Pterygioteuthis microlampas*, a 40-mm *Pyroteuthis addolux*, and a 26-mm *Abraliopsis* sp. B. The data for *P. microlampas* were the most scattered,



Figures 3a, b, c

Percent female gonad dry weight/total body dry weight plotted against dorsal mantle length for the three species studied.

perhaps due to a proportionally greater hydration error in the gonad weights of the small specimens during dry weighing.

The presence of spermatophores in the sperm receptacles of females of the larger size classes revealed that most had mated prior to capture. In *Pterygioteuthis microlamp-*

*pas*, spermatophores were usually found in females  $\geq 15$  mm DML. Spermatophores were usually found in female *Pyroteuthis addolux* and *Abraliopsis* sp. B  $\geq 35$  and 20 mm DML respectively; however, an occasional specimen of *P. addolux* as small as 14 mm DML, an *Abraliopsis* sp. B of 11 mm DML, also were found bearing spermatophores.

Fecundity, ovum sizes, and G/S ratio data from the largest individuals captured are summarized in Table 1. *Pterygioteuthis microlampas* differed from the other species in its reproductive pattern of high relative fecundity and smaller ova. The number of yolked ova per gram dry body weight in *P. microlampas* was approximately  $2.9\times$  that of *P. addolux*, and  $2.8\times$  that of *Abraliopsis* sp. B. Both differences were statistically significant ( $P < .05$ , Mann-Whitney test). The largest ova of *P. microlampas* measured 60% of the maximum ovum diameter of the other species.

Ova size-frequency data (Figure 4) were similar for the three species regardless of the method used. Typically, the percentage of yolked ova ( $\geq 300 \mu\text{m}$ ) found in the larger size classes increased with increasing G/S ratios. However, only a minority of ova fell within the largest size classes ( $>700 \mu\text{m}$ ), even in individuals with the highest G/S ratios. Ova  $700 \mu\text{m}$  or larger did not exceed 25% of the total number of yolked ova in any specimen. Non-yoloked oocytes ( $<300 \mu\text{m}$ ) accounted for an average of 63% (range 44–80%,  $n = 10$ ) of all oocytes present. Therefore, only a very small percentage of the total number of oocytes present had developed into mature ova in any of the specimens examined.

The sex ratios for adult *Pterygioteuthis microlampas*, *Pyroteuthis addolux*, *Pterygioteuthis giardi*, and *Abraliopsis* spp. A and B did not differ significantly from 1:1 (99% confidence limits from TATE & CLELLAND, 1957). In the rarely captured *Abralia trigonura*, 10 of 13 specimens were females.

## DISCUSSION

Although most of the adult female enoploteuthids examined in the present study had mated prior to capture, the generally low G/S ratios and scarcity of larger ova raise the question of whether full reproductive maturity was observed. Mating prior to full ova maturation has been reported for other squid species including *Loligo opalescens* Berry, 1911 (FIELDS, 1965) and *Todarodes pacificus* Steenstrup, 1880 (SOEDA, 1956 *vide* FIELDS, 1965, as *Ommastrephes sloani* Berry, 1912), and may also occur in Hawaiian enoploteuthids. According to FIELDS (1965), transfer of spermatophores in *L. opalescens* can occur "soon after the first few ova mature while the bulk of the gonad products are still unripe."

Despite the intensive sampling effort undertaken during the present study, the ripest females may have avoided capture. The problem of net avoidance by squid has been discussed by many authors (*e.g.*, HARDY, 1965; PEARCY, 1965; ROPER & YOUNG, 1975). Also, ROPER (1977) has

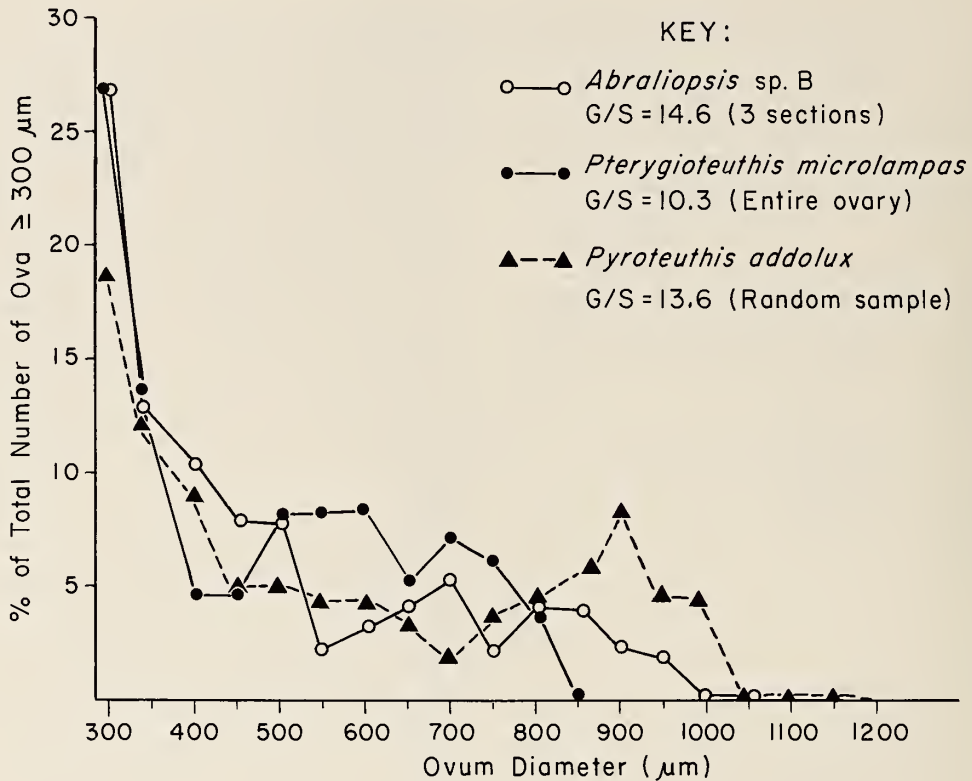


Figure 4

Typical ova size-frequency data for the three species studied. Distribution of ova expressed as the percentage of each size class relative to all ova  $\geq 300 \mu\text{m}$ .  $n = 1$  specimen for each curve. Species, % gonad dry weight/total body dry weight (G/S), and sampling method are indicated for each curve.

demonstrated that cephalopod capture rates and catch compositions vary with different types of midwater trawls. Unfortunately, the bias of the present samples cannot be specified because there is no unbiased method with which to compare them. It is noteworthy that the extent of net avoidance by enoploteuthids seems to be less than that of other, more powerful species. In the present study, although the ommastrephid *Symplectoteuthis oualaniensis*

(Lesson, 1830) was frequently observed in the study area, neither juveniles nor adults of this fast swimming species were captured by trawl. In contrast, adult enoploteuthids were captured occasionally even in the SB plankton tows. Spawning specimens also may have avoided capture by migrating into deeper waters or shallow coastal waters to spawn. Shoreward spawning migrations are known in other squid species, including the enoploteuthid *Watasenia*

Table 1

Fecundity, ovum sizes and gonad dry weight/total dry weight ratios of three enoploteuthid species. (Data from largest individuals captured)

Species	n	Individual fecundity (No. yolked ova) $\bar{x} \pm \text{SE}$	Relative fecundity $\left(\frac{\text{No. yolked ova}}{\text{Gram dry body weight}}\right)$ $\bar{x} \pm \text{SE}$	Largest ovum diameter $\mu\text{m}$	Gonad dry weight Total dry weight $\bar{x} \pm \text{SE}$
<i>Pterygioteuthis microlampas</i>	11	259 $\pm$ 45.5	4641 $\pm$ 712.5	900	0.096 $\pm$ 0.010
<i>Pyroteuthis addolux</i>	10	1259 $\pm$ 205.5	1609 $\pm$ 168.5	1300	0.108 $\pm$ 0.014
<i>Abraliopsis</i> sp. B	10	476 $\pm$ 39.8	1675 $\pm$ 149.5	1300	0.141 $\pm$ 0.013

*scintillans* Berry (SASAKI, 1914). Alternatively, if these species mature rapidly and complete spawning in a short period relative to their life span, or form spawning aggregations, the chances of sampling them at this stage would be quite small.

Female *Loligo opalescens* can lose more than 50% of their dry body weight at spawning, approximately 40% being weight lost by the reproductive system (FIELDS, 1965). In a mature *Octopus maya* (Voss and Solis, 1966), 34% of the dry body weight was attributable to dry egg matter (VAN HEUKELEM, 1976). In this study, the highest G/S ratio was observed in a specimen of *Abraliopsis* sp. B. Only 21% of the dry body weight was attributable to dry ovary weight. The average G/S ratios recorded (Table 1) were much lower. The low G/S ratios could indicate that partially spent or spawning females were captured. However, in other species for which information is available, large numbers of non-yolked oocytes are not usually present in the ovaries of spawning individuals. SASAKI (1914) noted that most of the ova of spawning *Watasenia scintillans* were "mature" and that a comparatively small number of immature ova were imbedded in the ovarian tissue; unfortunately, his criteria of egg maturity were not specified. KNIPE & BEEMAN (1978) found that the ovaries of spawning *L. opalescens* differed cytologically from immature ovaries in lacking pre-oocytes, which were defined as oögonia smaller than approximately 59  $\mu\text{m}$ . In the present study, non-yolked oocytes predominated, a large proportion of which were comparable in size to the pre-oocytes of KNIPE & BEEMAN (1978).

If the most mature specimens were not avoiding capture, the low G/S ratios and ova size distributions could suggest that these species have the potential to spawn repeatedly. In most species of cephalopods, death follows mating and spawning (ARNOLD & WILLIAMS-ARNOLD, 1977). In the enoploteuthids studied, the non-yolked oocytes may represent potential modes of ova for future spawning. Further studies are clearly required before conclusions may be drawn concerning the reproductive habits of these species.

Young *Pterygioteuthis microlampas* were most often captured during spring months, indicating a seasonal spawning tendency in this species. Seasonal spawning in one or more species also is suggested by the peaks observed in enoploteuthid larval abundance during fall and early winter months. If the 10–12 mm juveniles of *P. microlampas* which dominate the spring catch were spawned in the fall, a growth rate of 1.8–2.0 mm/month can be conjectured for juveniles of this species. Seasonal spawning also has been reported in other enoploteuthid species. *Watasenia scintillans* spawns in Toyama Bay, Japan in late spring and early summer (SASAKI, 1914). In a study of pelagic cephalopods from Oregon, seasonal spawning in a species of *Abraliopsis* was suggested by the predominance of small individuals in summer trawl samples (PEARCY, 1965).

The higher fecundity of *Pterygioteuthis microlampas* relative to other Hawaiian enoploteuthid species may be re-

lated to its seasonal spawning tendency. The production of greater numbers of offspring could function to offset the risk of high mortality should spawning coincide with conditions not favorable to larval survival.

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